

# FLOWERS FROM THE EOCENE OIL-SHALE OF MESSEL: A PRELIMINARY REPORT

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## ABSTRACT

A polycarpous flower perhaps belonging to the Magnoliales, a tiliaceous flower, and a male, branched, sapindalean inflorescence are described from the Middle Eocene oil-shale at Messel near Darmstadt, Germany.

## OIL-SHALE OF MESSEL

The oil-shale of Messel, located northeast of Darmstadt (Federal Republic of Germany), occupies an area of about 1 km in diameter and, like a few other small oil-shale deposits in the neighborhood, is surrounded by lower Permian sediments. All are tectonic trenches that originated during sinking of the Rhine valley during the early Tertiary.

The Messel oil-shale originally had a thickness of more than 150 m before it was mined. During mining a large collection of plant and animal fossils were assembled. Among the animal fossils, the vertebrates are of particular significance because they are very well preserved, sometimes showing fine details such as skin, hairs, and feathers (Koenigswald, 1980). The vertebrates are also important for the determination of the age (Lutetian, Middle Eocene; Tobien, 1968), and the occurrence of crocodiles has been taken as indicating a tropical to subtropical climate (Berg, 1966). Like the vertebrates, other fossils such as insects and plant leaves are also well preserved, and there is the potential for reconstructing much of the fauna and flora of the "Messel lake" through further investigations. Because of plans to fill the open cast mine with refuse, the Forschungsinstitut Senckenberg, Frankfurt am Main, and several other institutes have been actively collecting from the locality.

## PLANT FOSSILS

Plant fossils, especially leaves, were collected during the mining period. They were first described by Engelhardt (1922) and deposited in the Hessische Landesmuseum Darmstadt and in the Forschungsinstitut Senckenberg, Frankfurt

am Main. A more recent revision of the Lauraceae from the locality is published by Sturm (1971). One of the difficulties in preserving the Messel fossils is that the oil-shale splits into small fragments during drying. Recently however, the transfer of animal specimens onto synthetic resins has allowed larger specimens to be salvaged. In the last few years, we have collected a lot of new plant material that consists mainly of leaves; but also fruits as well as five flowers have been collected. Plant remains are not distributed homogeneously in the oil-shale, but there is no area in the mine where a special leaf layer can be found. The leaves occur singly and scattered throughout the sediment and, due to their rarity, we have collected only about 3,000 over the last seven years. During this period several new techniques for their preparation and investigation have been devised (Schaarschmidt, 1982).

The quality of preservation of the leaves is quite variable but can be easily gauged with the use of epi-fluorescence microscopy. Some have well-preserved cuticles but in others the cuticles had been more or less destroyed by decay before fossilization. The water of the Messel lake had little current (Franzen, 1982), and therefore the leaves may have been very slowly deposited. For the same reason flowers are seldom preserved and those present are of fairly large size.

In this paper, I present a preliminary report of the first three flowers, which were found in Messel until 1980. Since this time, the number of collected specimens increased enormously. Particularly, excavations during the summers of 1983 and 1984 brought a lot of small flowers, and by help of fluorescence, it was possible to identify insignificant remains. The more than 1,000 flowers collected so far belong to about 70 genera of several families.

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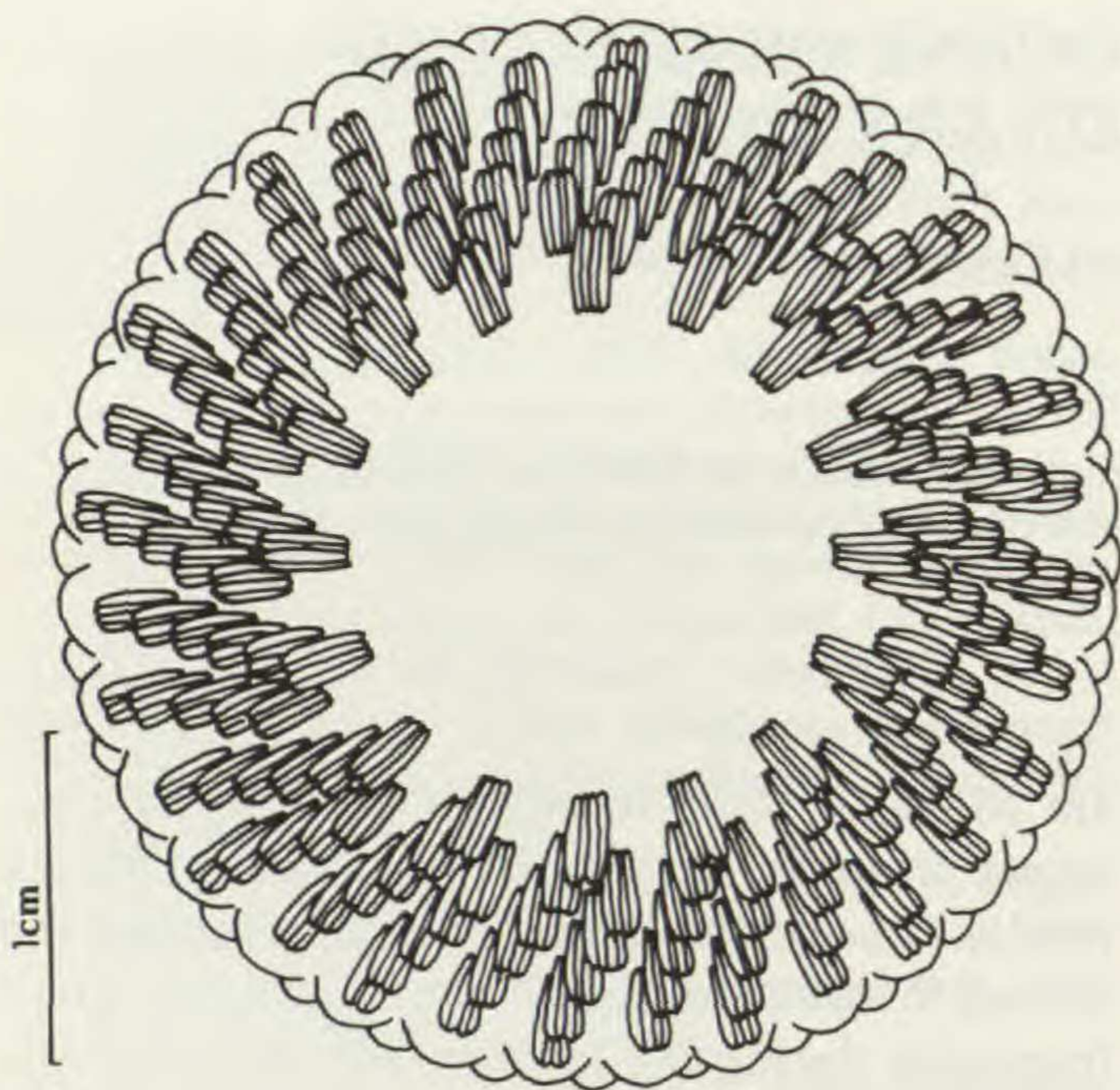


FIGURE 1. Reconstruction of the Magnoliales flower;  $\times 2$ .

#### TECHNIQUE

Engelhardt (1922) published only drawings of the leaves, as did Sturm (1971) using an improved drawing technique, because of the difficulties of photographing the black leaves on the black oil-shale. Frequently it is not easy to see the leaf margin or the venation of dry prepared specimens. We have tried several techniques for examining the leaves, and some of these have also been helpful for the study of the flowers (Schaarschmidt, 1982).

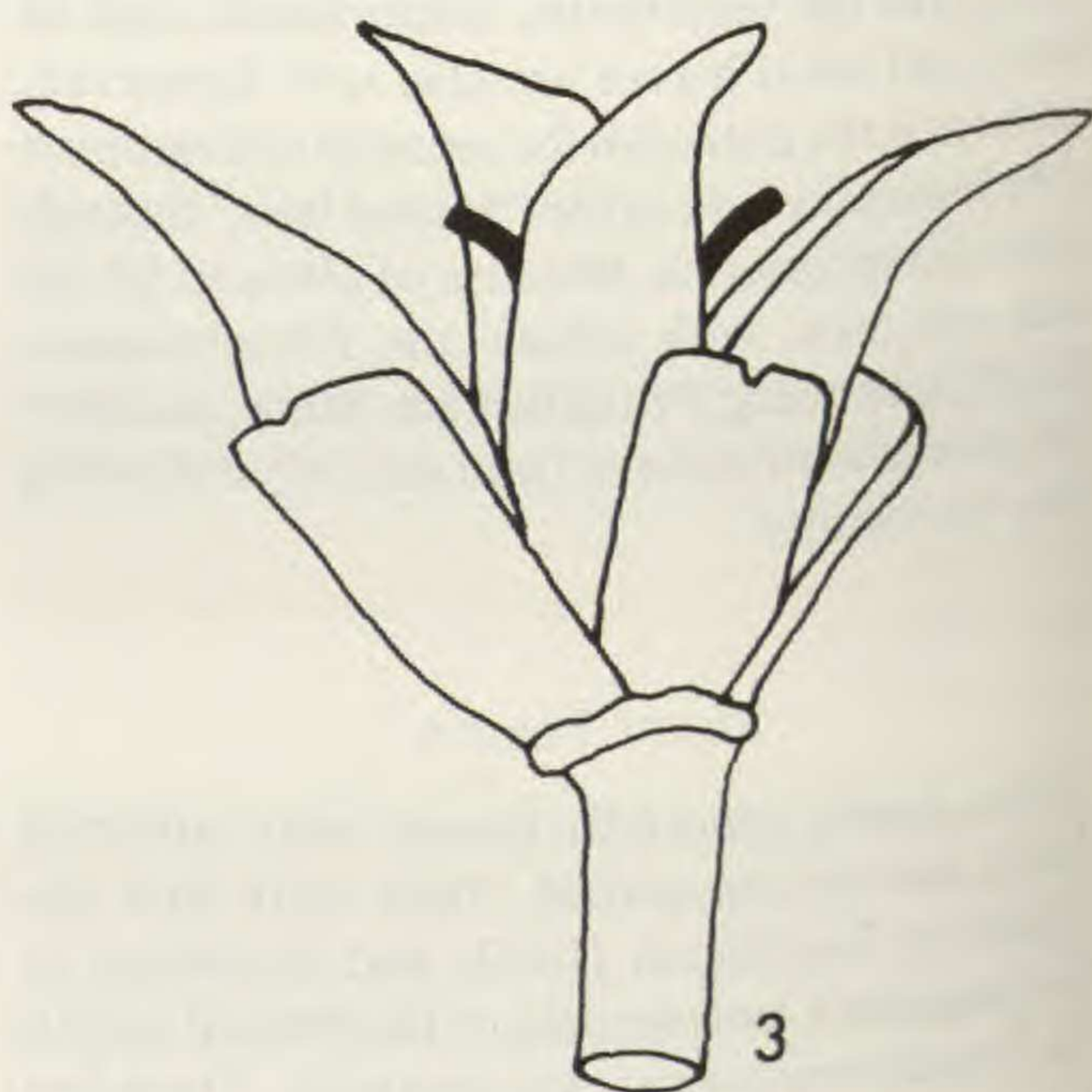
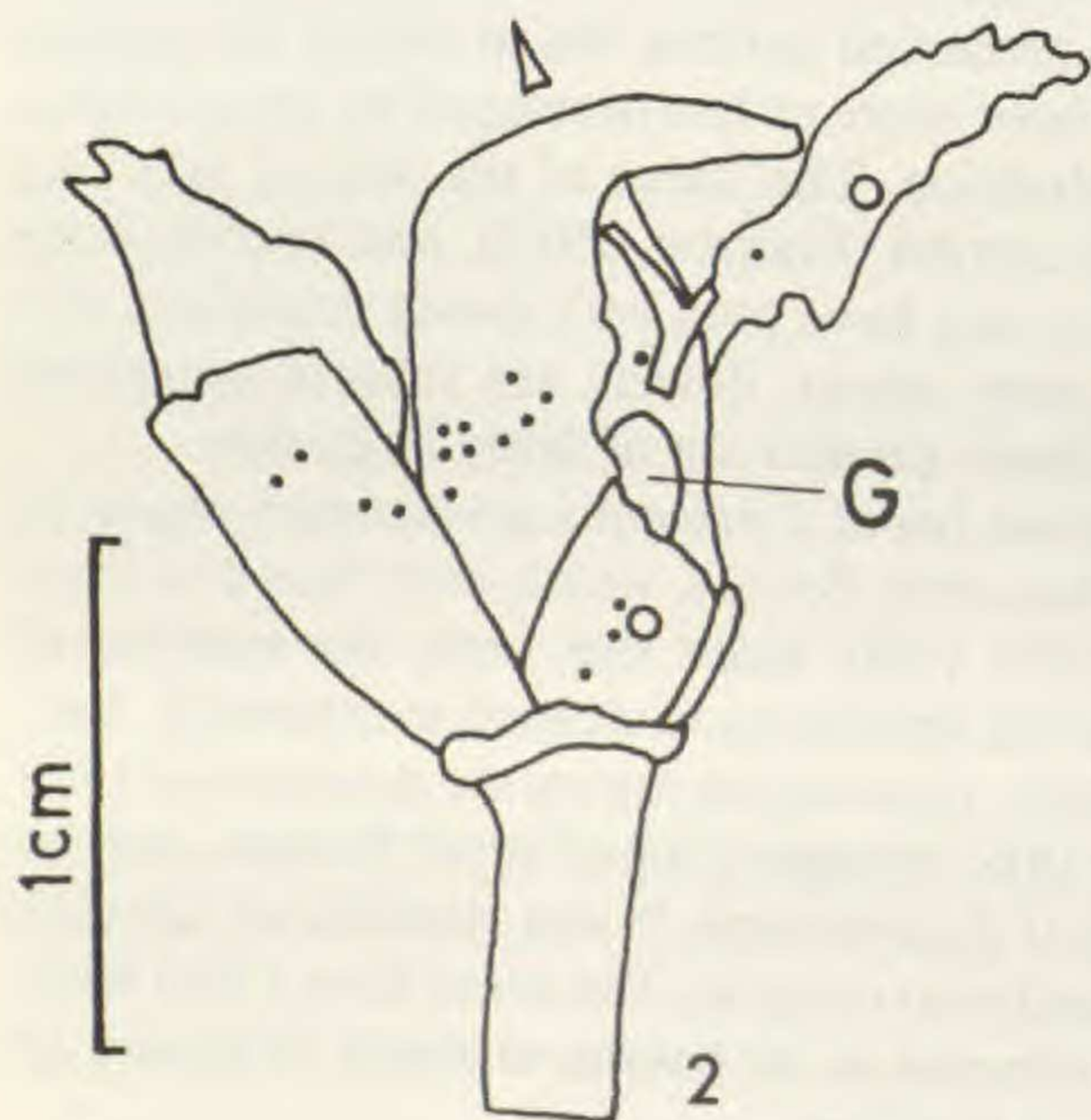
Because the Messel oil-shale breaks during drying, the flowers and other delicate samples are stored in a fluid, either glycerine (disinfected by Thymol) or in liquid Polyethylene-Glycol 200, 400, or 600. Specimens stored in this way are easy to photograph. If necessary, contrast was increased by two polarizing filters, one attached at the lamp, the other below the camera objective (Schaarschmidt, 1973). For one specimen, we obtained clear pictures in infrared light by use of the Wild infrared image intensifier M 520, provided for testing by Ernst Leitz KG, Frankfurt am Main. For fine details, we successfully used the fluorescence technique (Friedrich & Schaarschmidt, 1977, 1979) and were able to observe grains, either isolated or in the anthers, sufficiently well for preliminary determination. Anther wall details could also be seen with this technique.

We have constructed special macrofluorescence equipment for lower power observation (Schaarschmidt & Friedrich, 1981, Schaarschmidt, 1982). At the microscope, we have used the following filters: for excitation, a band pass filter, BP 350–460 and as barrier filter, a long-wave pass filter, LP 515.

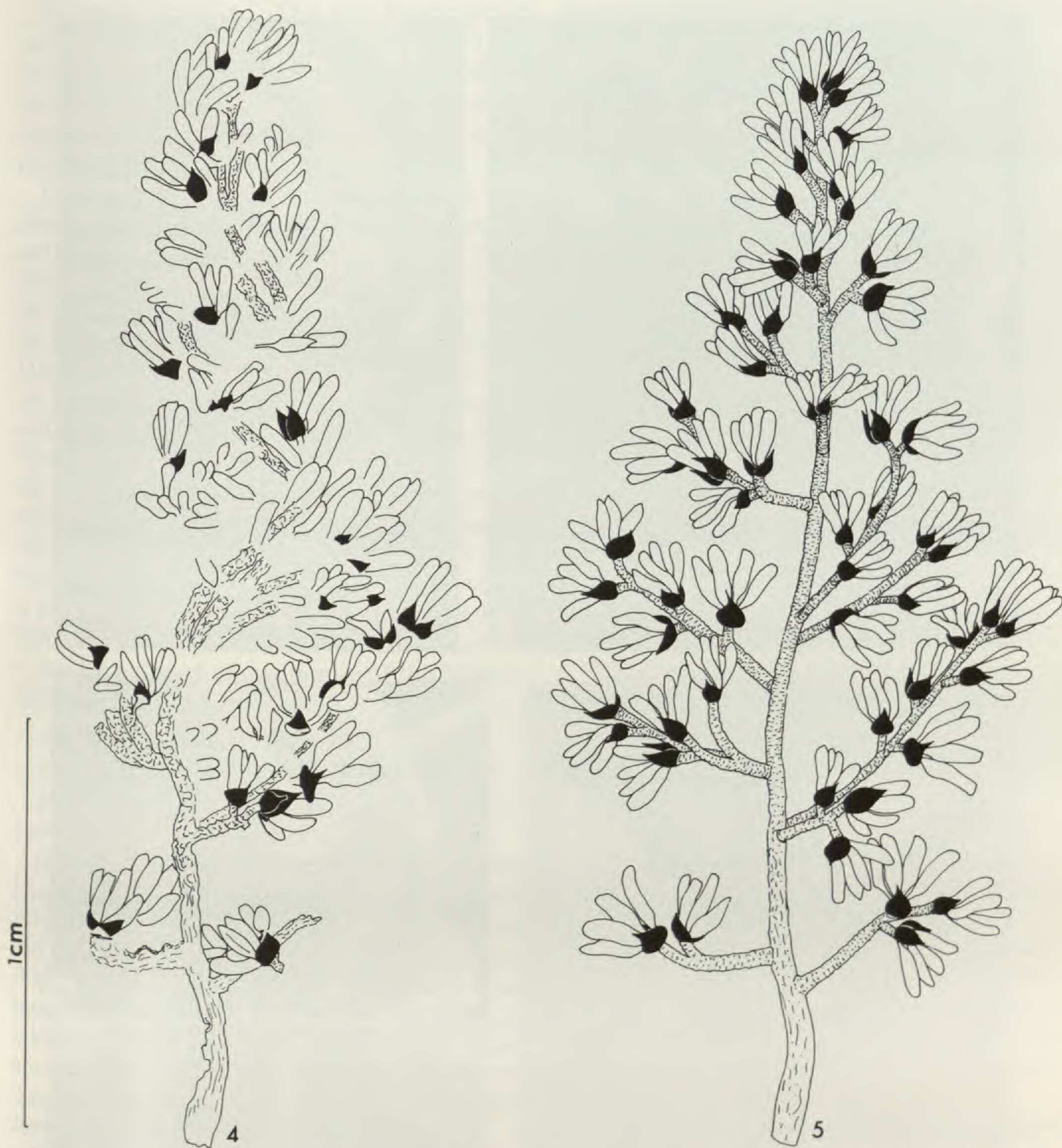
#### MAGNOLIALES FLOWER

*Material.* Forschungsinstitut Senckenberg, SM.B. 13476.

*Description.* The fragment of a disc-like flow-



FIGURES 2, 3. Tiliaceae flower;  $\times 3$ .—2. Drawing according to the fossil. Three sepals (one complete), 4 petals, ovule (G) and style visible (points = single pollen grains, circles = groups of pollen grains).—3. Reconstruction.



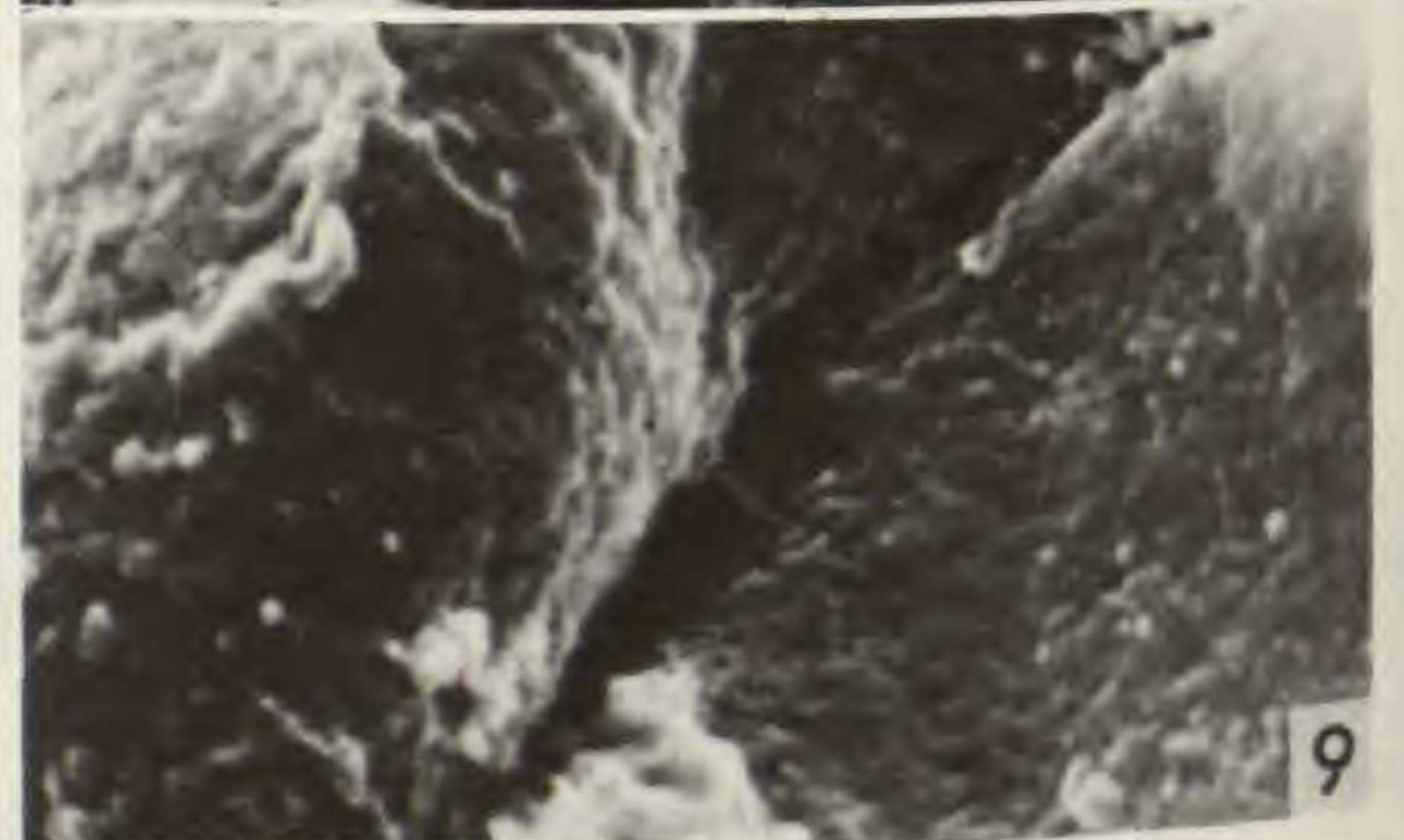
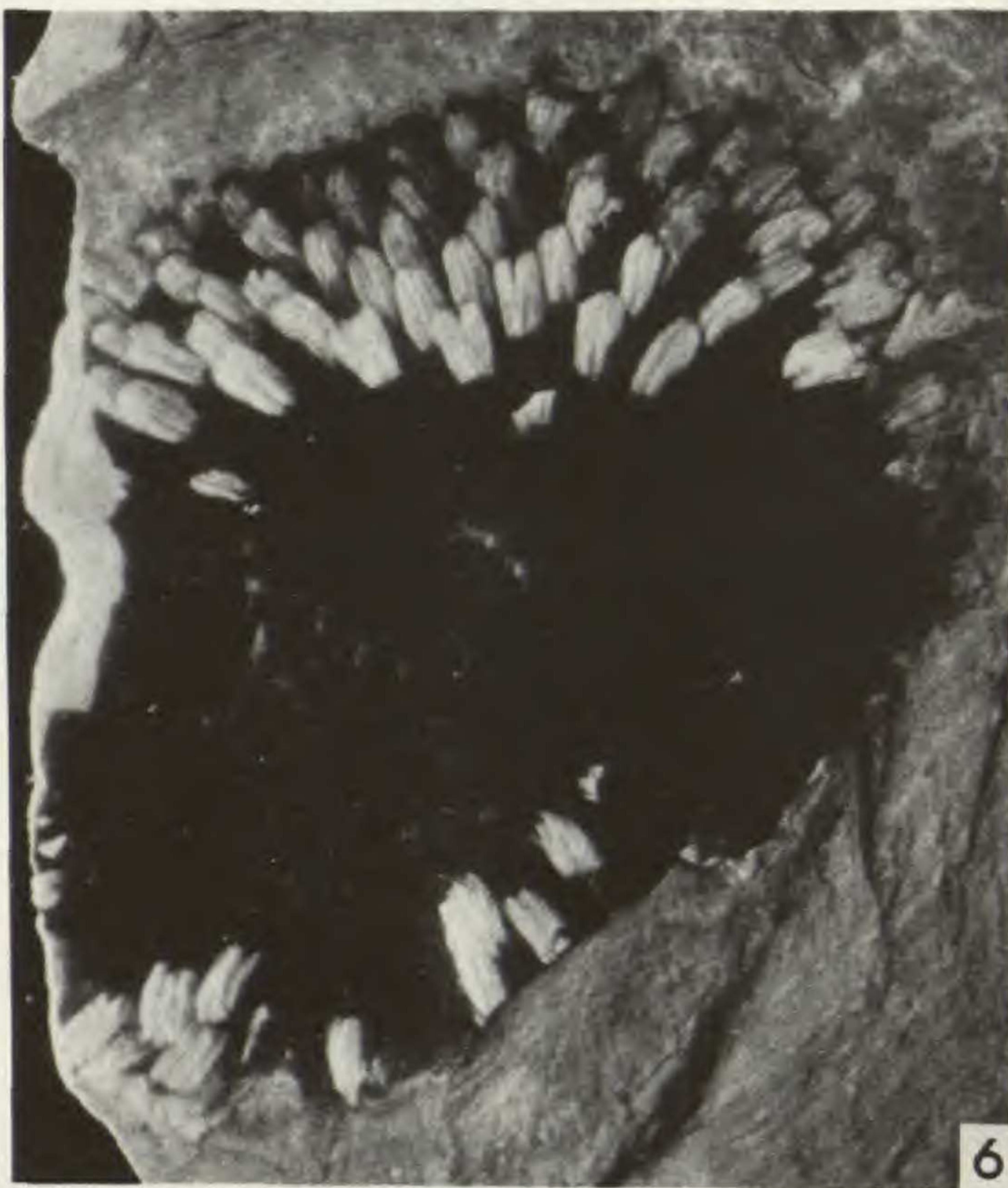
FIGURES 4, 5. Sapindales inflorescence;  $\times 5$ .—4. Drawing according to the fossil; main axis broken in the middle part and drifted to the right; scales black.—5. Reconstruction.

er has a diameter of 32 mm and shows two groups of helically arranged stamens (Figs. 1, 6). In infrared and fluorescent light, the anthers are clearly seen to consist of four thecae (2–2.5 mm long), which open by a long longitudinal slit (Fig. 7). The filament is attached basally or dorsally. The perianth has an unknown number of rounded parts and is not much longer than the stamens (Fig. 7). It is not possible to decide whether these are sepals or petals. If carpels were present they must have been in the center of the flower, where the fossil is absolutely black. In this area, there

seems to be some indistinct objects shaped like *Ranunculus* carpels.

The pollen grains are clearly visible in fluorescent light. Isolated grains are distributed all over the flower, and the pollen sacs are full, suggesting fossilization before anthesis. The prolate tricolporate pollen grains average 22  $\mu\text{m}$  in diameter. The three equatorial colpi have indistinct pores and the exine is fine scabrate (Figs. 8–11).

A reconstruction of the flower is given in Figure 1.



FIGURES 6-13. 6-11. Magnoliales flower.—6, 7. The specimen in infrared light; 6,  $\times 2.5$ ; 7,  $\times 5$ .—8. Scanning electron micrograph of the polar view of a pollen grain;  $\times 2,500$ .—9. Scanning electron micrograph of the structure

*Systematic position.* This type flower occurs only in the Polycarpicae (Ranales sensu lato), but there seems to be no family that includes all the following features of the specimen: helical arrangement of the stamens, long thecae, a short perianth, and tricolporate pollen grains.

The first two characteristics occur in the Nymphaeaceae, but generally they have longer petals and inaperturate or monosulcate pollen. Tricolporate pollen occurs in *Nelumbo* (Erdtman, 1952: 287). The same arrangement and construction of the stamens also occur in the Magnoliales. In the Magnoliaceae, the pollen grains are monosulcate, but tricolporate pollen does occur in the Illiciaceae and Schisandraceae (Erdtman, 1952: 254–258). Flowers of some Dilleniaceae are also similar; the Dilleniaceae produce tricolporate pollen grains (Erdtman, 1952: 148) and in the Paeoniaceae tricolporate pollen is found. Despite these similarities, without knowledge of the gynoecium it is not possible to assign the flower to an extant family. However, at least, in so far we know it, it may be a flower of one family of the Magnoliales.

#### TILIACEOUS FLOWER

*Material.* Landessammlungen für Naturkunde, Karlsruhe, 1 flower.

*Description.* Flower with a pedicel 15 mm long, four pointed and recurved petals. Three petals are obvious and the tip of a fourth petal can be seen at the upper margin of the flower (Figs. 2, 3, 12). The petals may have been thin, because they are folded. In front of the left and middle petals are remains of two sepals. They are strap-shaped. Ovary and style are preserved but still covered by parts of the flower. No stamens are visible.

Pollen grains are scattered on the surface of the calyx. These pollen grains are all of one morphological type (Fig. 13). The grains are tripore-ovate and of the tilioid type. Because of their uniformity and because of the absence of other different pollen grains, I believe that they were produced by this flower, which would also indicate bisexuality. The pollen grains are 36–42  $\mu\text{m}$  (average 39.5  $\mu\text{m}$  diameter) and rounded to triangular in outline in polar view. The tilioid

pores are located at the straight flank (i.e., plan-aperturate).

*Systematic position.* The systematic position is clearly identified by the pollen as tilioid type pollen, which occur only in the Tiliaceae (Mai, 1961: 56), although not in all genera of the family. On the other hand, most of the flowers in this family are pentamerous, but a few subfamilies such as the Tetralicoideae and the Tilioideae pro parte (e.g., *Sparmannia*) are tetramerous (Burret, 1926).

Mai (1961) described a flower of the Tiliaceae: *Burretia instructa* Mai (Brownlowioideae) from the Miocene of Central Germany, but this is quite different from the Messel fossil. It is pentamerous, unisexual, and has a fused calyx. The Messel flower is tetramerous, bisexual, and has free sepals, and may belong to a genus of the Tilioideae with tetramerous flowers but not to *Sparmannia*, which does not have tilioid pollen grains. Also, the *Tilia* flowers described by Hall and Swain (1971) have no similarity to the Messel flower.

Tilioid pollen is abundant in the Tertiary. At Messel, *Intratropopollenites pseudinstructus* Mai (1961, text-fig. 3), occurs in the dispersed palynoflora and is similar to the pollen grains found in the flower.

#### SAPINDALES INFLORESCENCE

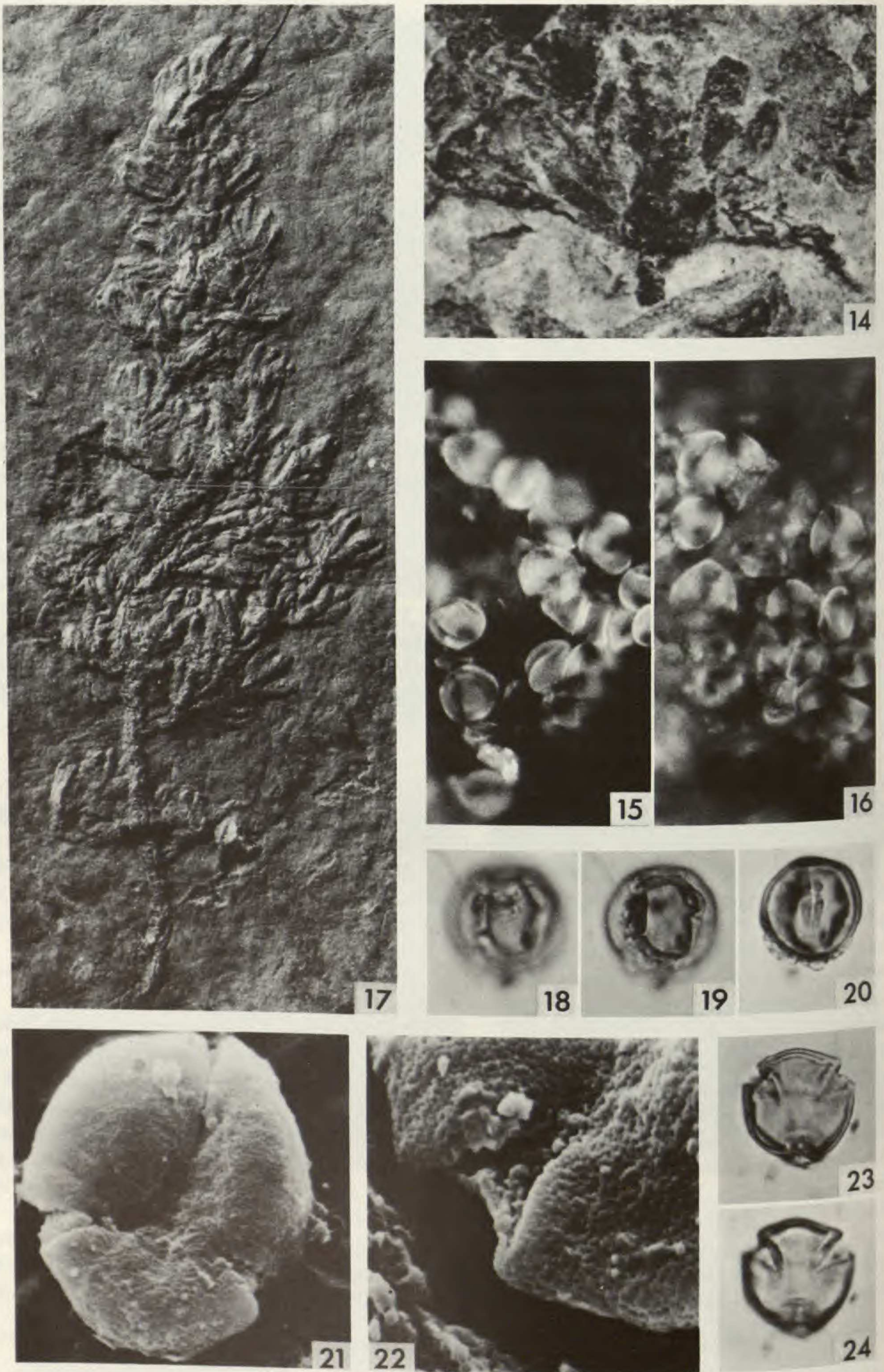
*Material.* Forschungsinstitut Senckenberg, SM.B. 13477.

*Description.* The specimen is a catkin 28 mm long consisting only of stamens. In the lower part it is branched several times. The middle part is broken, slightly distorted, and displaced to the right, perhaps by a weak current during deposition (Figs. 4, 5, 14).

The stamens are arranged in groups, which may be simple flowers (Fig. 15). Unfortunately, it is impossible to count the exact number of the stamens but the number appears to be between three and six. Each flower has one or two pointed scales about 1 mm long at the base. The scales are not conspicuous and both can be seen only in laterally compressed flowers.

The anthers are 2.5 mm long, with a short filament. They open by longitudinal slits. In fluorescent light the epidermis of the anthers is vis-

of the colpus and the exine;  $\times 5,000$ .—10, 11. Polar and lateral views of the pollen grains in transmitted light;  $\times 1,000$ . 12, 13. Tiliaceae flower.—12. The whole specimen;  $\times 3$ .—13. Polar view of a pollen grain, epi-fluorescence;  $\times 500$ .



FIGURES 14-24. Sapindales inflorescence.—14. Cluster of flowers, the scale of one flower visible;  $\times 20$ .—15, 16. Pollen grains in stamens, epi-fluorescence;  $\times 500$ .—17. The specimen in flat light;  $\times 5$ .—18-20, 23, 24. Pollen

ible and consists of longitudinal cells. The epidermis of the scales has polygonal cells.

The pollen grains are fairly small, 18  $\mu\text{m}$  in diameter, circular in equatorial and polar views, and distinctly tricolporate (Figs. 15–24).

*Systematic position.* Because of the very simple construction, it is not easy to find the right position of the inflorescence. There are two orders of angiosperms that come into question. Both have bisexual flowers but with the tendency to unisexuality and wind pollination.

In one order, Hamamelidales, the single flower of the Messel inflorescence resembles most the Cercidiphyllaceae, which also has flowers with two scales at the base. But in contrast to our specimen, the inflorescences of the Cercidiphyllaceae are close clusters, they have more stamens per "flower" (8–11), and their pollen grains are only tricolpate (Erdtman, 1952: 106–107). The other families of Hamamelidales, Platanaceae, and Hamamelidaceae, are still more different, as well, in their flowers and pollen grains, especially in the construction of the inflorescences, which are normally clusters or globose heads. Only a few genera of Hamamelidaceae have spikes, but none have branched catkins. The related Eucomiaceae also have simple perianthless male flowers. The pollen grains are 3-colporoidate (Erdtman, 1952: 164), but the flowers are also in clusters. It seems that the Messel inflorescence does not belong to the Hamamelidales or any related family.

The second order with a tendency towards unisexuality are the Sapindales. Most families have panicle-like inflorescences, occasionally with unisexual flowers that lack a perianth. It seems that the most similar inflorescences occur in the following families. Several genera of Sapindaceae have paniculate inflorescences. The male flowers of *Dodonaea*, for instance, contain about seven stamens, petals are absent but the four small, conspicuous sepals don't correspond with our flowers. More similar are the male catkin of *Pistacia* (Anacardiaceae). The five stamens are of similar shape and size, and at the base of the single flowers a scale-like bract is visible. However, the flowers of *Pistacia* have a reduced 5-lobed calyx. It may be that the flowers of the

Messel inflorescence also had a calyx before fossilization. On the other hand, the relationship to *Pistacia* is not probable, because in this genus the catkins are not branched and the pollen grains are different: they normally have more than three "not sharply delimited" apertures (Erdtman, 1952: 48).

There are still more families in the Sapindales in which unisexual panicles occur—sometimes the flowers without petals—for instance: Staphyleaceae, Sabiaceae, Burseraceae, Simaroubaceae, and Meliaceae. But we have not yet found a living genus that includes all attributes of the Messel inflorescence. Therefore, we classify it as a Sapindales inflorescence.

#### CONCLUSIONS

There is, with a few exceptions, a long gap between the excellent published record of fossil flowers by Conwentz (1886) from the Eocene Baltic amber and the modern systematic investigation of early Tertiary flowers, especially from the Middle Eocene Clairborne formation by Crepet, Dilcher, and others. It is rapidly becoming clear that fossil flowers are available for investigation and yield important information for our understanding of angiosperm evolution. It seems that, by the early Tertiary, anemophilous flowers were already highly developed, and at nearly the same level of their living relations (Crepet, 1979)—e.g., Juglandaceae (Crepet et al. 1975), Fagaceae (Crepet & Daghighian, 1980), and Ulmaceae (Zavada & Crepet, 1981). Against that, the entomophilous flowers have still been more primitive. Therefore, it is generally not as easy as in the anemophilous flowers to compare them with living plants. Most of the fossil entomophilous flowers are radially symmetrical; bilateral symmetry is still at the beginning. It is also significant that the fossil record of early angiosperms shows both catkins and oligomerous radial flowers. Polycarpous flowers are found rarely as fossils generally. For instance, Seward and Conway (1935: 22. pl. 4. fig. 20) and Bock (1962, text-figs. 498, 499) published seed axes called *Magnoliaestrobis* from Cretaceous of Greenland and Oligocene of Hungary; Dilcher (1979: 315. figs. 40, 50, 51) and Dilcher and Crane (1984)

← grains in lateral and polar view in transmitted light;  $\times 1,000$ .—21. Scanning electron micrograph of the polar view of a pollen grain;  $\times 2,500$ .—22. Scanning electron micrograph of the structure of the colpus and the exine;  $\times 5,000$ .

have described an archaic elongated axis with a high number of carpels from the middle Cretaceous. Now in Messel the male part of a flower of this important plant group is first found, which was interpreted as the most primitive angiosperm group by many botanists in the past.

Although in the Messel oil-shale flowers are very rare, we hope to contribute more results to this important field of angiosperm paleobotany in the future, because the plant remains of Messel are well preserved and allow several fine-detailed investigations.

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